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Taxonomic study of the alpine carabid beetle *Nebria* (*Falcinebria*) *taketoi* Habu, 1962 (Coleoptera, Carabidae)

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Abstract

The carabid beetle *Nebria taketoi* Habu, 1962 is endemic to the high-altitude mountains of Honshu, Japan; due to its rarity, it is one of the least taxonomically studied species among Japanese *Nebria*. This study taxonomically revised *N. taketoi* based on morphological comparisons, mainly of the endophallus in males, and geometric morphometrics of the pronotum, a taxonomically useful external character. Specimens previously identified as *N. taketoi* were found to belong to at least two species: *N. taketoi*, with a currently confirmed distribution in the northern Hida Mountains (type locality: Mikurigaike, Mount Tateyama), and *N. kobushicola* **sp. nov.** from the Okuchichibu and Yatsugatake mountains (type locality: Mount Kobushigatake). Species identities in populations from other localities could not be determined, as male specimens for endophallus examinations were unavailable. However, some populations may consist of species distinct from *N. taketoi* and *N. kobushicola*, based on their distribution and morphometric features. Based on comparative morphology of the endophallus, *N. kobushicola* shares features more similar to *N. niohozana* Bates, 1883 and *N. dichotoma* Sasakawa, 2020 than to *N. taketoi*.

Key Words

endophallus, Japan, male genitalia, new species description, taxonomy

Introduction

Nebria taketoi Habu, 1962 is a Japanese endemic species of the beetle family Carabidae found in high-elevation areas in the mountains of central Honshu. It is one of the least studied Japanese species of the genus *Nebria*, mainly due to its rarity. To date, there are only a few collection records, and public collections contain a limited number of specimens (e.g., Yoshitake et al. 2011; Yoshimatsu et al. 2018). Moreover, studies of *N. taketoi* have been hindered by the complicated nomenclatural history of this species and the resulting misunderstandings. Specifically, two of the three papers on the taxonomy of this species were written in Japanese (Uéno 1953; Nakane 1974), such that the nomenclature has been incorrectly understood by researchers outside Japan (Farkač and Janata 2003; Ledoux and Roux 2005; Huber 2017).

This study performed a taxonomic revision of *N. taketoi* based on two types of analyses that have been performed in some *Nebria* taxa but not in *N. taketoi*: a comparative morphology of the endophallus (the membranous inner sac everted from the aedeagus) of the male genitalia, which when fully inflated often have a complex shape that provides taxonomic information; and geometric morphometrics, which can quantitatively evaluate subtle morphological differences that are difficult to detect via traditional morphometrics (e.g., aspect ratios). The utility of these two approaches in species- and supra-species-level taxonomies has been demonstrated in some *Nebria* taxa (e.g., Huber et al. 2010; Sasakawa 2016; Huber and Schnitter 2020), including *Nebria reflexa* Bates, 1883 and its relatives, which belong to the same subgenus as and are closely related to *N. taketoi*

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(Sasakawa 2000; Sasakawa and Itô 2021). Therefore, the two analytical approaches were employed in this study to clarify the taxonomy of *N. taketoi*.

Materials and methods

Materials

Specimens treated as *Nebria taketoi* or *N. nakanei* Uéno, 1953 and housed in the collections of the following institutions or individuals in Japan were examined: Gifu Prefectural Museum, Seki-shi, Gifu Prefecture (**GPM**); the Hokkaido University Museum, Sapporo, Hokkaido (**HUM**); Kenta Sawada, Toyama-shi, Toyama (**KSWD**); the National Agriculture and Food Research Organization, Tsukuba-shi, Ibaraki (**NARO**); and Tateyama Caldera Sabo Museum, Tateyama-machi, Toyama (**TCSM**). Label data of the *N. taketoi* holotype were provided in the original notation without any modification; a slash (/) was used to separate lines on the same label, and a double slash (//) to separate different labels. Label data (i.e., locality and collection date) of other specimens, which were often written in a simplified, older notation, were modified to be compatible with the more-detailed, currently used notation whenever possible.

Among the collection sites, Murôdodaira is only 70 m from the type locality, Mikurigaike, and was therefore regarded as being virtually the same site as the type locality. In total, 10 male and 17 female specimens from 14 sites, ranging from the Iide Mountains in the north to Mount Kitadake (Akaishi Mountains) in the south and Mount Ontakesan in the west, were examined (Fig. 1).

Comparative morphology

Body length was measured from the mandible apices to the elytral end based on scaled dorsal-view photographs taken with a digital camera, using the software ImageJ ver.

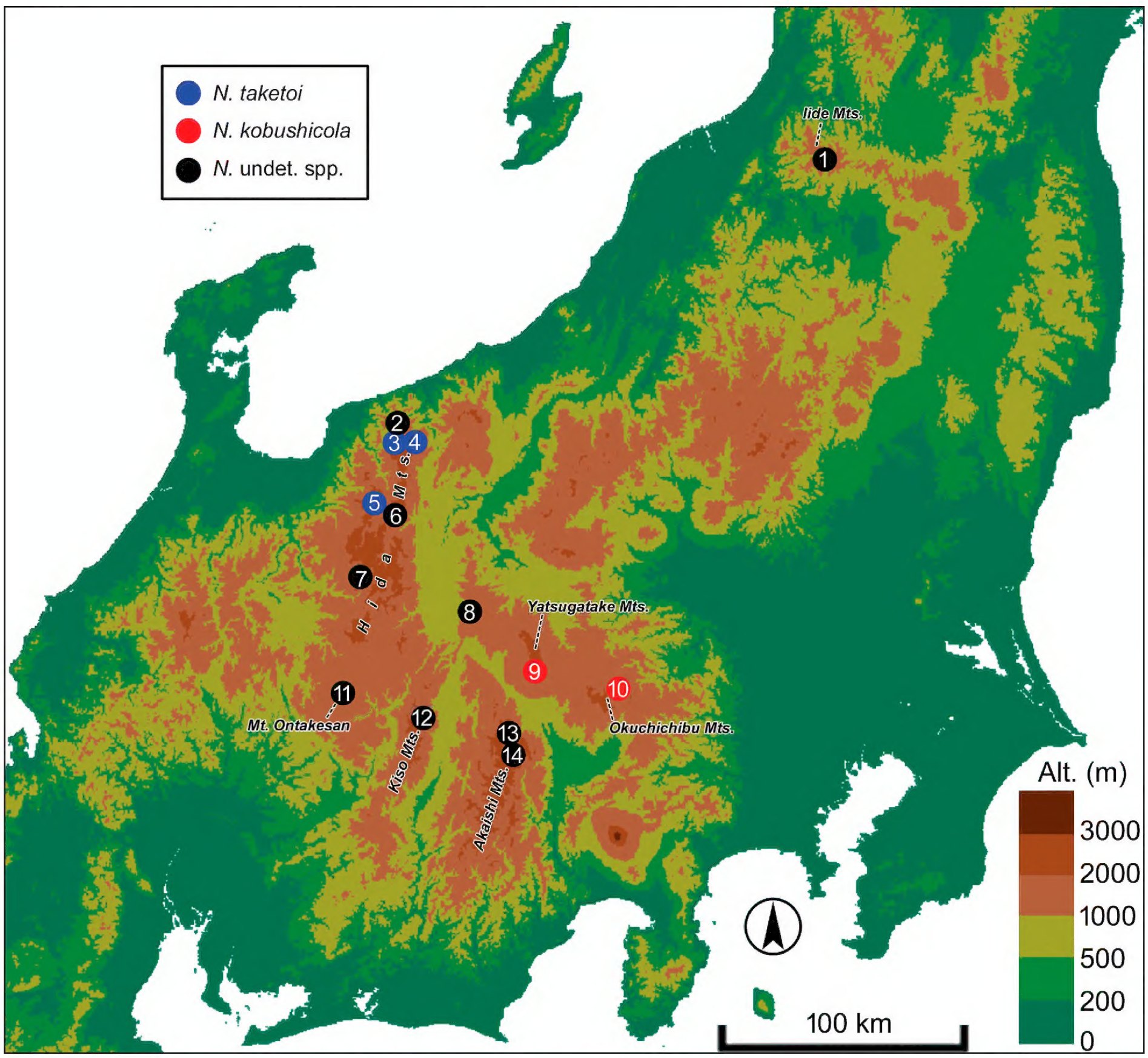

Figure 1. Collection sites of the examined specimens. Locality numbers correspond to those in Fig. 6.

1.50i (Rasband 2016). Measurements and subsequent calculations [mean and standard deviation (SD)] were performed using values with an accuracy of 0.001 mm, but values with an accuracy of 0.01 mm are reported in the species descriptions. The endophallus was everted and fully inflated by injecting toothpaste from the base of the aedeagus. In some specimens, toothpaste injection into the gonopore protrusion and some lobes was difficult, such that these structures could not be fully everted. This was also the case in consubgeneric *N. reflexa* and allied species, and particularly for their gonopore protrusion (Sasakawa 2020). To prevent damage to these structures by toothpaste injection, the endophallus of the respective specimens was observed with the gonopore protrusion and lobes not fully everted. The homology and terminology of the endophallus structures were adopted from Sasakawa (2020).

Morphometric analyses

Geometric morphometrics were performed for the dorsal view of the pronotum. The utility of the shape of pronotum for species-level taxonomy has already been demonstrated in various groups of *Nebria* (Huber et al. 2010; Roggero et al. 2013; Sasakawa 2016, 2020; Huber and Schnitter 2020). Scaled digital images were obtained using a digital camera attached to a microscope. The pronotum was maintained with the apices of anterior and posterior angles of both lateral sides in the same horizontal plane when taking photographs. Using the software tpsDig version 2.17 (Rohlf 2013a), four points were plotted as landmarks, and 42 points distributed along the contour at regular intervals between landmarks were plotted as semi-landmarks (Fig. 2). The landmarks are as follows: 1, anterior end along the median line; 12, apex of anterior angle of the left side; 35, apex of hind angle of the left side; and 46, posterior end along the median line. The semi-landmarks are as follows: 2–11, between landmarks 1 and 12; 13–34, between landmarks 12 and 35; and 36–45, between landmarks 35 and 46. Using the software tpsRelw version 1.53 (Rohlf 2013b), the raw coordinates were converted into Procrustes coordinates, in which variations due to rotation, position and size were removed with semi-landmarks being 'slid' along the contours. Relative warp analysis and visualization of shape differences were also performed using this software. The raw data used in the analysis are provided in Suppl. material 1.

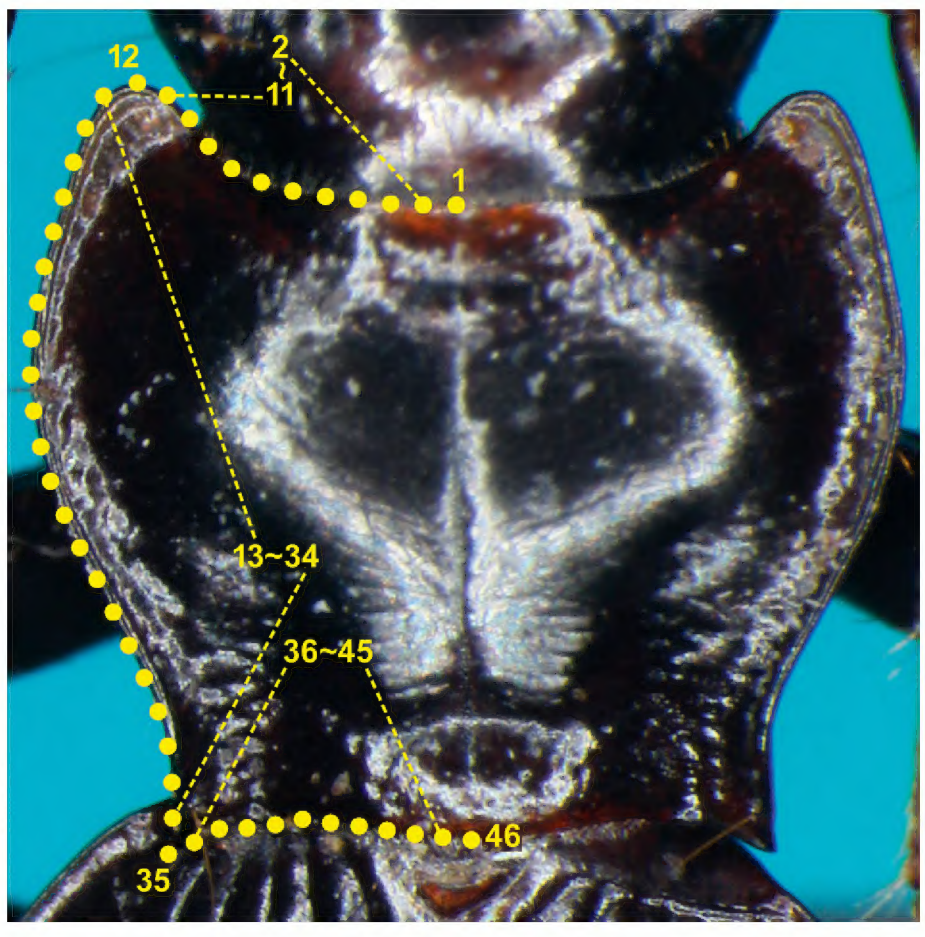

Figure 2. Positions of landmarks (1, 12, 35, and 46) and semi-landmarks (the others) on a pronotum.

Results

Comparative morphology revealed that specimens previously treated as *N. taketoi* included at least two different species (Fig. 1): *N. taketoi*, the currently confirmed distribution of which is the type locality (Mount Tateyama) and two high-altitude mountains in the northern Hida Mountains (Mount Shiroumadake and Mount Yukikuradake), and a species from Mount Kobushigatake (Okuchichbu Mountains) and Akadakekousen (Yatsugatake Mountains), described below as the new species *N. kobushicola*. These two species are distinguished by their external morphologies (Fig. 3) and by the morphology of the endophallus (Figs 4, 5).

The identities of the following specimens (2♂9♀) could not be determined due to the unavailability of male specimens from the same collection site, thus prohibiting endophallus examinations (male specimens were either absent or unsuitable for dissection): 2♀ (NARO), Iide Mountains, Niigata Prefecture, 21.vii.1976, K. Terada leg.; 1♀ (NARO), Mount Asahidake, Itoigawa-shi, Niigata Prefecture, 27.vii.1961, K. Baba leg.; 1♀ (NARO), "Ogawara", Mount Harinokidake, on the border between Tateyama-machi, Toyama Prefecture and Omachi-shi, Nagano Prefecture, 3.viii.1958, M. Kurata leg.; 1♀ (GPM), Kuriyadani Valley, 1600–2000 m, on the eastern side of Mount Shakujôdake, Takayama-shi, Gifu Prefecture, 22.viii.1985, K. Suzuki leg.; 1♀ (HUM), Iriyamabe, Matsumoto-shi, Nagano Prefecture, 28.vii.1943, K. Takahashi leg.; 1♀ (NARO), Mount Ontakesan, on the border between Nagano and Gifu prefectures, 19.vii.1961, S. Imafuku leg.; 1♀ (NARO), Kitagoshodani Valley, Miyada-mura, Nagano Prefecture, 5.viii.1960, Oobori leg.; 1♂ (NARO), Kitazawatôge Pass, Minamiarupusu-shi, Yamanashi Prefecture, 15.viii.1956, K. Fujii leg.; 1♂1♀ (NARO), Mount Kitadake, Minamiarupusu-shi, Yamanashi Prefecture, 15.viii.1956, K. Fujii leg.

In the geometric morphometrics (Fig. 6), the first relative warp scores (RW1) accounted for 32.8% of the total variance and was mainly associated with the contour of overall shape; positive and negative values indicated square and cordate shapes, respectively. The second relative warp scores (RW2) accounted for 20.5% of the total variance and was mainly associated with the shape of anterior angle; positive value indicated narrowly- and

strongly-protruding anterior angle, whereas negative value indicated widely-rounded and barely-protruding anterior angle. In the scatterplot of RW1 and RW2, the areas representing *N. taketoi* and the new species *N. kobushicola* did not overlap. None of the specimens with undetermined species identity were included in the areas of either *N. taketoi* and *N. kobushicola*, with the exception of the male specimen from Kitazawatôge Pass, which was just barely included in the male *N. taketoi* area.

In the following, a redescription of *N. taketoi* and a description of the new species, *N. kobushicola*, considered to be distinct based on the morphology of its endophallus, the external morphology, and a morphometric analysis, are provided.

Descriptions

N. taketoi and *N. kobushicola* are similar to each other and adults share the following morphology.

***Habitus*:** Dorsal surface of body glossy, not opaque; mouthpart appendages, legs, except for femora, reddish brown to brownish black; vertex with reddish brown patch; other body parts almost black.

***Head*:** Widest at mid-eye level. Mandibles stout, with the length between the apex and posterolateral end of the left mandible 1.5 times longer than the anterior width of the clypeus; apices of both left and right mandibles sharp; apex of the left mandible bent inward at a right angle, with the length of the apical part as long as the width of the apical end of the maxillary palp; inner margin of left mandible, except the apical part, only slightly arcuate; apex of right mandible not bent like the left one; inner margin of the right mandible arcuate, with a more arched curvature than the left mandible; one seta on the dorsolateral side. Labrum usually with three pairs of setae at the anterior margin, with additional one to two setae in some individuals; anterior margin slightly wavy, with anterolateral corners protruding anteriorly; area at the second outermost pair of setae concave, and area at the innermost pair of seta protruding anteriorly; middle of the anterior margin shallowly concave. Clypeus with a pair of setae. Frontal impressions shallow, wider than antennomere 1, reaching the supraorbital seta. Tempora short, not swollen. Eyes convex, with the anterior–posterior length twice as long as the width at the widest part as seen on dorsal view; width between apices of left and right eyes 1.4–1.5 times as wide as that between the inner margins of the eyes; posterior end of eyes behind the supraorbital seta, with the longitudinal length between the level of the supraorbital seta and that of the posterior end of the eye less than one-third the anterior–posterior length of the eye. Reddish brown patch on vertex slightly behind the level of the supraorbital setae. Antennomere 1 with one or two setae on apical quarter; antennomere 2 as long as half the length of antennomeres 1 and 3, without setae; antennomeres 3–10 with six setae on the subapical to apical part; antennomeres 5–11 with pubescence.

***Pronotum*:** Cordate-shaped, widest at apical one-third on the anteroposterior length between the levels of the anterior and hind angle apices. Dorsal surface smooth except for anterior, posterior, and lateral margins, which are more or less punctate. Lateral margin arcuate on apical seven eighths, with a contour more strongly arched than the curvature of the anterior and posterior margins and posterior one-eighth of the lateral margins; posterior one-eighth almost straight or only slightly sinuate. Anterior margin almost straight or only slightly arched anteriorly, except for lateral areas, which near the anterior angles are directed anterolaterally, at an angle of ~45°. Posterior margin almost straight or only slightly arched posteriorly; lateral areas near the posterior angles directed posterolaterally, at an angle of < 45° from the lateral direction. Anterior angles prominent anteriorly, with widely rounded apices. Hind angles with both sides almost straight, forming an acute angle; apices not denticulate. Anterior transverse impression grooved, but without a distinct line. Lateral margins narrow, with the width equal to or less than the length of antennomere 2. Median line distinctly impressed in the middle area, nearing but not connecting with the anterior and posterior margins. Laterobasal impressions single, deep, with the degree of concavity greater than that of the convexity of the median area of the pronotum; end of the anterior part reaching the apical half of the pronotum; impressions of both sides connected by a transverse groove; the degree of concavity of which is weaker than that of the laterobasal impressions and greater than that of the pronotum median line. Two marginal setae on each lateral side, anterior setae at widest pronotal point and posterior setae in front of hind angle.

***Elytra*:** Oblong, widest almost at the middle, convex. Shoulders indistinct, with elytral anterior and lateral margins smoothly connected, forming an arc. Elytral apices rounded, not denticulate. Distinct basal transverse line connecting anterior ends of elytral intervals. Scutellar stria present, not connected to stria 1; posterior end behind the posterior end of the scutellum. Stria distinct, impressed as strongly as the median line of the pronotum; intervals less convex; microsculpture transverse. Setigerous puncture either absent on stria 1 or present at or behind the level of the posterior end of the scutellum. Five or six setigerous punctures on interval 3, all adjoining or near stria 3. Around ten marginal setigerous punctures on interval 9. Hind wings atrophied.

***Ventral side*:** Ventral side of head smooth, except for gena in some specimens, in which ventrolateral sides of the gena have more than five shallow, somewhat indistinct transverse wrinkles. Mentum with three pairs of setae, one near the tooth, one at the middle part near the posterior margin, and one at the posterolateral margins; mentum tooth shallowly bifid; submentum with > 16 setae along the anterior margin. Ventral side of pronotum almost smooth except for prosternum and pleuron; prosternum near the anterior margin and anterolateral corners and the pleuron punctate. Mesepisternum, mesepimeron,

and metepisternum, more or less punctate in all specimens. Sternites II–III punctate in some specimens. Sternites IV–VII almost smooth in all specimens. Metepisternum subparallelogram, with lateral margins > 1.7 times as long as the basal width. Metacoxa with two setae; medial seta absent. Metatrochanter without setae. Sternites IV–VI with two to six setae on each lateral side. Sternite VII with two to three setae on each lateral side in males, three to four setae in females.

***Legs*:** Slender, with hind tibia about twice as long as the width of the pronotal posterior margin. Apical outer end of hind tarsomere 4 distinctly protruding posteriorly but short; length difference between the inner and outer ends on ventral view equal to or less than the width of the basal end of hind tarsomere 5. Hind tarsomere 5 with four to five setae on ventrolateral margins.

***Male genitalia*:** Aedeagus stout and strongly arcuate; apex short and widely rounded. Endophallus with five lobes on the surface in both species, two on the laterobasal surface (laterobasal lobes), two on the lateroapical surface (lateroapical lobes), and one on the dorsoapical surface (dorsoapical lobe); surface around the gonopore protruding (gonopore protrusion). Both right and left parameres spatulate, with the former larger than the latter.

Nebria (*Falcinebria*) *taketoi* Habu, 1962

Figs 3A, B, E, F, I, J, 4

Nebria taketoi Habu: Habu (1962): 2 (original description, type locality "Mikurigaike, Mt. Tateyama, Toyama Prefecture", subgenus *Paranebria*); Nakane (1974): 15 (part, subgenus not specified); Farkač and Janata (2003): 94 (subgenus *Paranebria*); Ledoux and Roux (2005): 831 (misidentified type locality "Japon, mont Yatsuga-take", subgenus *Falcinebria*); Yoshitake et al. (2011): 4 (subgenus *Paranebria*); Yoshitake et al. (2011): 34 (part, subgenus *Falcinebria*); Huber (2017): 50 (misidentified type locality "Yatsudatake Mts.", subgenus *Falcinebria*); Yoshimatsu et al. (2018): 38 (part, subgenus *Falcinebria*).

Nebria nakanei Uéno: Uéno (1953): 58 (unavailable name under International Code of Zoological Nomenclature (ICZN) article 8.3, specimen(s) from "the Azusagawa River, Kamikôchi", subgenus *Paranebria*); Nakane (1963): 19 (part, subgenus *Paranebria*); Ledoux and Roux (2005): 832 (subgenus *Falcinebria*); Huber (2017): 50 (synonym of *taketoi*).

Notes. In his brief review of Japanese *Nebria*, Uéno (1953) reported on a species of *Nebria* referred to as *Nebria nakanei* based on specimen(s) from Kamikôchi in the Hida Mountains, with a comment that the species would later be formally described as a new species. However, a description of *N. nakanei* was never published. Habu (1962) described *Nebria taketoi* based on a male from Mount Tateyama in the Hida Mountains; this species is apparently identical to *N. nakanei*. In his brief review of Japanese *Nebria*, Nakane (1974) treated this species under the name *N. taketoi* and stated that it is most likely conspecific with *N. nakanei*. That report included a line drawing of the pronotum of an individual from the Yatsugatake Mountains. This complicated nomenclatural history was not correctly understood by researchers outside Japan, in part because the reports by Uéno (1953) and Nakane (1974) were written in Japanese. In Ledoux and Roux (2005), the type locality of *N. taketoi* was described as the Yatsugatake Mountains, and *N. nakanei* was treated as a related species of *N. taketoi*. This was probably due to the misidentification of the Yatsugatake Mountains, whose specimen was described by Nakane (1974), as the same as the type locality of *N. taketoi*. In the Catalogue of Palaearctic Coleoptera, which is widely accepted by experts, *N. taketoi* and *N. nakanei* are treated as the same species under the name of *N. taketoi*, but the reason for this classification is not provided (Farkač and Janata 2003; Huber 2017). The type locality was again given as the Yatsugatake Mountains. Since Uéno (1953) himself did not intend to describe this species in his publication, the nomenclature of *N. nakanei* used in that report was not accepted according to ICZN article 8.3, such that *N. nakanei* remains an unavailable name. Therefore, *N. taketoi* should be used as the name of this species, and its type locality is "Mikurigaike, Mt. Tateyama," as stated in Habu (1962).

Materials examined. ***Holotype*** ♂ (NARO), "VIII. 5, 1961 / Mikurigaike / Mt. Tateyama / Toyama P. / A. TAKETO // Holotype / Nebria. / taketoi / HABU"; 2♂5♀ [1♂3♀ (KSWD), 1♂2♀ (TCSM)], Murodôdaira, alt. 2390 m, Ashikuraji, Tateyama-machi, Nakaniikawa-gun, Toyama Prefecture, Japan (36°34'43"N, 137°36'6"E), 27.viii.2019, Kenta Sawada leg.; 1♂1♀ (NARO), Renge-Onsen, Mount Shiroumadake, Itoigawa-shi, Niigata Prefecture, Japan, 29.vii.1977, K. Baba leg.; 1♂ (NARO), Mount Yukikuradake, Itoigawa-shi, Niigata Prefecture, 26.vii.1961, K, Baba leg.

Diagnosis. *Nebria taketoi* is distinguished from the new species described below by less protruded anterior angles of the pronotum, more densely punctated pronotal margin and the ventral sides of some of its notal and abdominal segments, and not bifurcated apices of lateroapical and dorsoapical lobes of the endophallus. Among specimens previously treated as *N. taketoi*, the absence of setigerous punctures on elytral stria 1 is a character found only in individuals of *N. taketoi*. However, due to individual variation, in which setigerous punctures are seen in a few individuals, the presence of this character does not provide a definitive diagnosis at the individual level.

Description. ***Body length*:** ♂, 10.29–10.94 mm (mean ± SD: 10.62 ± 0.28 mm, n = 5); ♀, 10.42–12.16 mm (mean ± SD: 11.31 ± 0.65 mm, n = 6).

***Head*:** Dorsal surface smooth, except for frontal impressions, the surfaces of which are more or less wrinkled. Antennomere 1 usually with one seta, rarely two setae.

***Pronotum*:** Surface near and in front of anterior transverse impression moderately punctate but clearly lacking punctations near the anterior margin; surfaces of lateral margins, laterobasal impressions, and area between the transverse groove and the posterior margin moderately punctate.

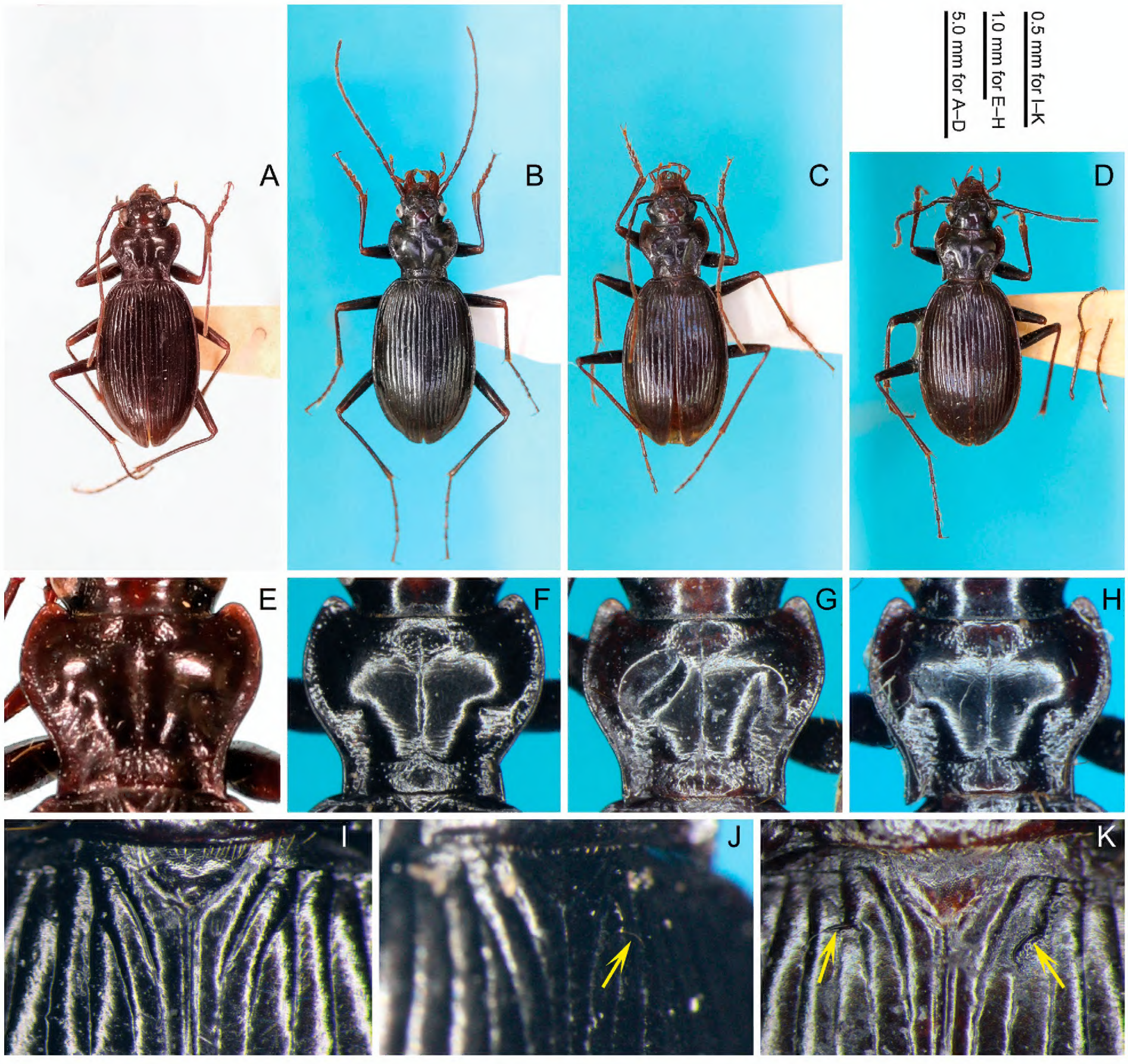

Figure 3. External structures of *Nebria taketoi* and *N. kobushicola* sp. nov. **A, E.** *N. taketoi* holotype male from Mikurigaike; **B, F, J.** *N. taketoi* male from Murodôdaira; **I.** *N. taketoi* female from Murodôdaira; **C, G, K.** *N. kobushicola* holotype male from Mount Kobushigatake; **D, H.** *N. kobushicola* paratype male from Mount Aka; **A–D.** Habitus, in dorsal view; **E–H.** Pronotum, in dorsal view; **I–K.** Elytral base around the median line in dorsal (**I, K**) and left dorsolateral (**J**) views, showing the variation [present (yellow arrows) or absent (no arrow)] in setigerous puncture on stria 1.

***Elytra*:** Anteroposterior length between the level of the basal transverse line and that of the posterior end of the scutellar stria more than twice as long as the anteroposterior length between the level of the basal transverse line and that of the posterior end of the scutellum. Setigerous punctures on stria 1 variable at the individual level, including one on both sides, one on either side, and absent on both sides.

***Ventral side*:** Submentum with 16–25 setae. Surface punctations of prosternum near the anterior margin and anterolateral corners and pleuron sparser than those at the pronotal laterobasal impressions. Mesosternal, metasternal, and abdominal surface almost smooth, except for mesepisternum, mesepimeron, metepisternum, metasternum, and metacoxa for all specimens examined, and sternite II for some specimens. All surfaces of the mesepisternum, mesepimeron, and metepisternum, and the lateral side of the metasternum until the metepisternum punctate to the same degree as pronotal laterobasal impressions. Metacoxae punctate at lateral sides, with the degree of punctation varying among individuals, ranging from only a few punctations to the same degree as the metepisternum; in all cases, punctures weaker than those of the mesepisternum, mesepimeron, and metepisternum. Punctures of sternite II varying from absent to punctation as extensive as on other notal parts. Sternites IV–VI with three to six setae on each lateral side. Male sternite VII with two setae on each lateral side.

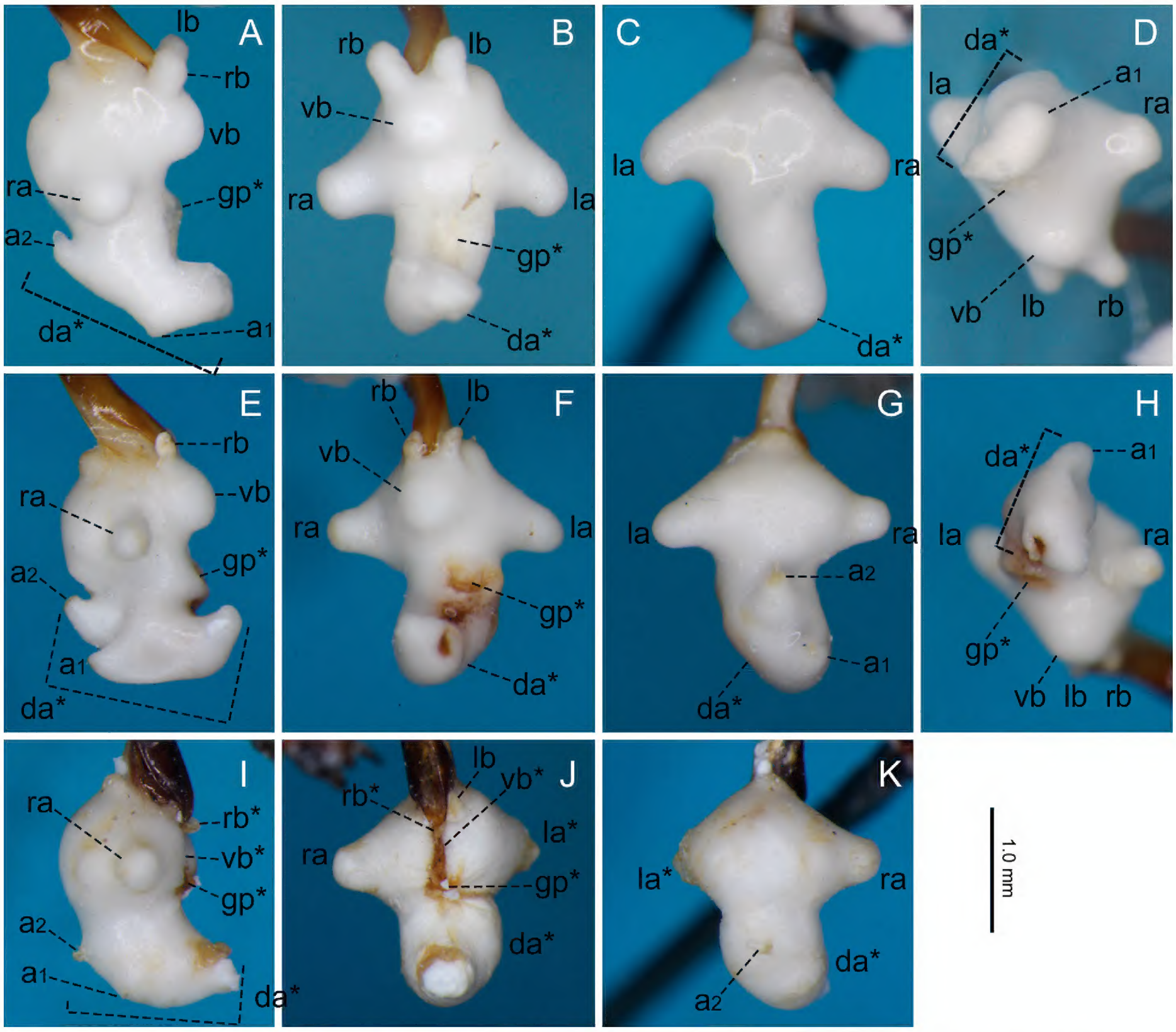

Figure 4. Endophallus of *Nebria taketoi*. **A–D.** Male from Murodôdaira; **E–H.** Male from Mount Yukikuradake; **I–K.** Male from Renge-Onsen. Right lateral view (**A, E, I**), ventral view (**B, F, J**), dorsal view (**C, G, K**), and ventroapical view (**D, H**), showing a dorsal view of the dorsoapical lobe. Abbreviations: da. dorsoapical lobe, gp. gonopore protrusion, la. left lateroapical lobe, lb. left laterobasal lobe, ra. right lateroapical lobe, rb. right laterobasal lobe, vb. ventrobasal swelling. a_1 and a_2 denote apices of the dorsoapical lobe. Asterisk indicates that the gonopore protrusion or lobes is not fully everted.

***Male genitalia*:** Laterobasal lobes semi-ellipsoid, with the basal diameter smaller than the height; inflated lobes directed ventrobasally, covering the aedeagal apex on lateral views. Lateroapical lobe broadly rounded at apex, directed lateroapically, not bent, and larger than the laterobasal lobes. Dorsoapical lobe with two protrusions on dorsobasal and dorsomedian parts; protrusions weakly bent, directed basally, and smaller than the lateroapical lobes; apex of the protrusions narrowly rounded; in the specimens examined, the dorsoapical lobe apex was not fully inflated, but its shape is probably broadly rounded or slightly widened. Ventrobasal swelling large and semi-spherical on lateral views; basal diameter larger than that of laterobasal lobes. Dorsobasal surface near the ostium with a lobe smaller than the ventrobasal swelling. Gonopore protrusion probably present, but unsuccessfully inflated in the specimens examined.

Nebria (*Falcinebria*) *kobushicola* Sasakawa, sp. nov.

https://zoobank.org/F38997DD-D669-4E26-8134-C97F43FFB284

Figs 3C, D, G, H, K, 5

Nebria taketoi Habu: Nakane (1974): 15 (part, subgenus not specified); Yoshitake et al. (2011): 34 (part, subgenus *Falcinebria*).

Types. ***Holotype*:** ♂ (NARO), Mount Kobushigatake, Chichibu-shi Saitama Prefecture, 3.viii.1963, S.-I. Uéno leg. Paratypes: 1♂2♀ (NARO), same data as the holotype; 1♂ (HUM), Akadakekousen, alt. ca. 2240 m, the Yatsugatake Mountains, Chino-shi, Nagano Prefecture, 25.vii.1956, F. Motoyoshi leg.

Diagnosis. This new species is distinguished from *N. taketoi* by more protruded anterior angles of the pronotum, less punctated pronotal margin and ventral sides of some notal and abdominal segments, and bi-

furcated apices of lateroapical and dorsoapical lobes of the endophallus.

Description. ***Body length*****:** ♂, 10.78–11.08 mm (mean ± SD: 10.88 ± 0.17 mm, n = 3); ♀, 11.11–11.82 mm (mean ± SD: 11.47 ± 0.51 mm, n = 2).

Head**:** Dorsal surface smooth; antennomere 1 with one seta.

Pronotum**:** Surfaces of anterior transverse impression, lateral margins, laterobasal impressions, and area between the transverse groove and posterior margin only sparsely punctate.

Elytra**:** Anteroposterior length between the level of the basal transverse line and that of the posterior end of the scutellar stria > 4 times longer than the anteroposterior length between the level of the basal transverse line and that of the posterior end of the scutellum. One setigerous puncture on stria 1.

Ventral side**:** Submentum with 16–20 setae. Punctations of prosternum surfaces near anterior margin and anterolateral corners and pleuron denser than or as dense as those at the pronotal laterobasal impressions. Mesosternal, metasternal and adominal surface almost smooth except for mesepisternum, mesepimeron, and metepisternum for all specimens examined, and metasternum and sternite II for some specimens. All surfaces of mesepisternum, mesepimeron, and metepisternum punctate to the same degree as or more densely than the pronotal laterobasal impressions. Punctures of metasternum (lateral sides) and sternite II (anterolateral sides) varying among individuals, ranging from absent to the same as on other notal parts. Sternites

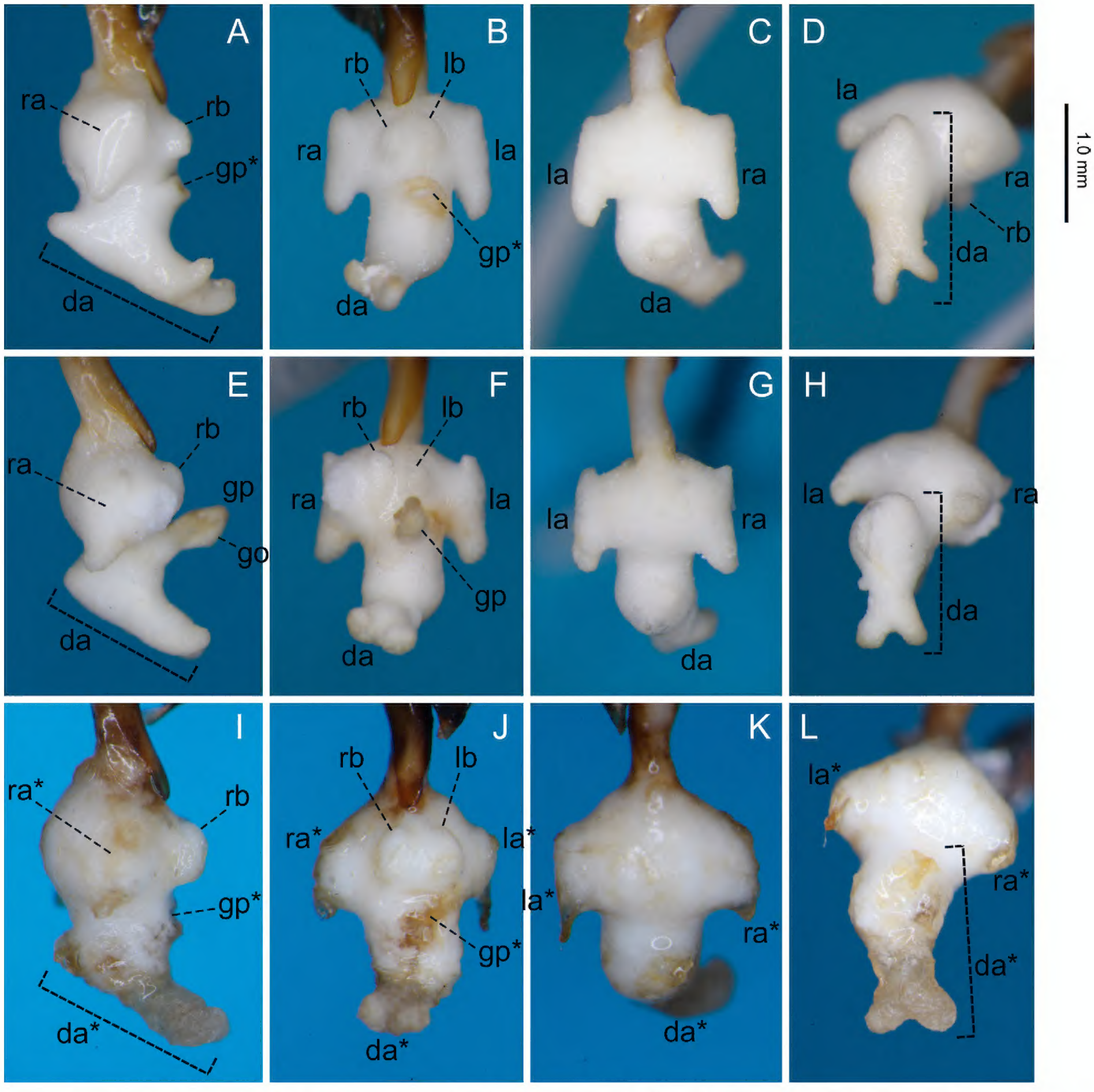

Figure 5. Endophallus of *Nebria kobushicola* sp. nov. **A–D.** Holotype male from Mount Kobushigatake; **E–H.** Paratype male from Mount Kobushigatake; **I–L.** Paratype male from Akadakekousen. Right lateral view (**A, E, I**), ventral view (**B, F, J**), dorsal view (**C, G, K**), and dorsoapical view (**D, H, L**), showing a dorsal view of the dorsoapical lobe. Abbreviations: go, gonopore; others are the same as in Fig. 4.

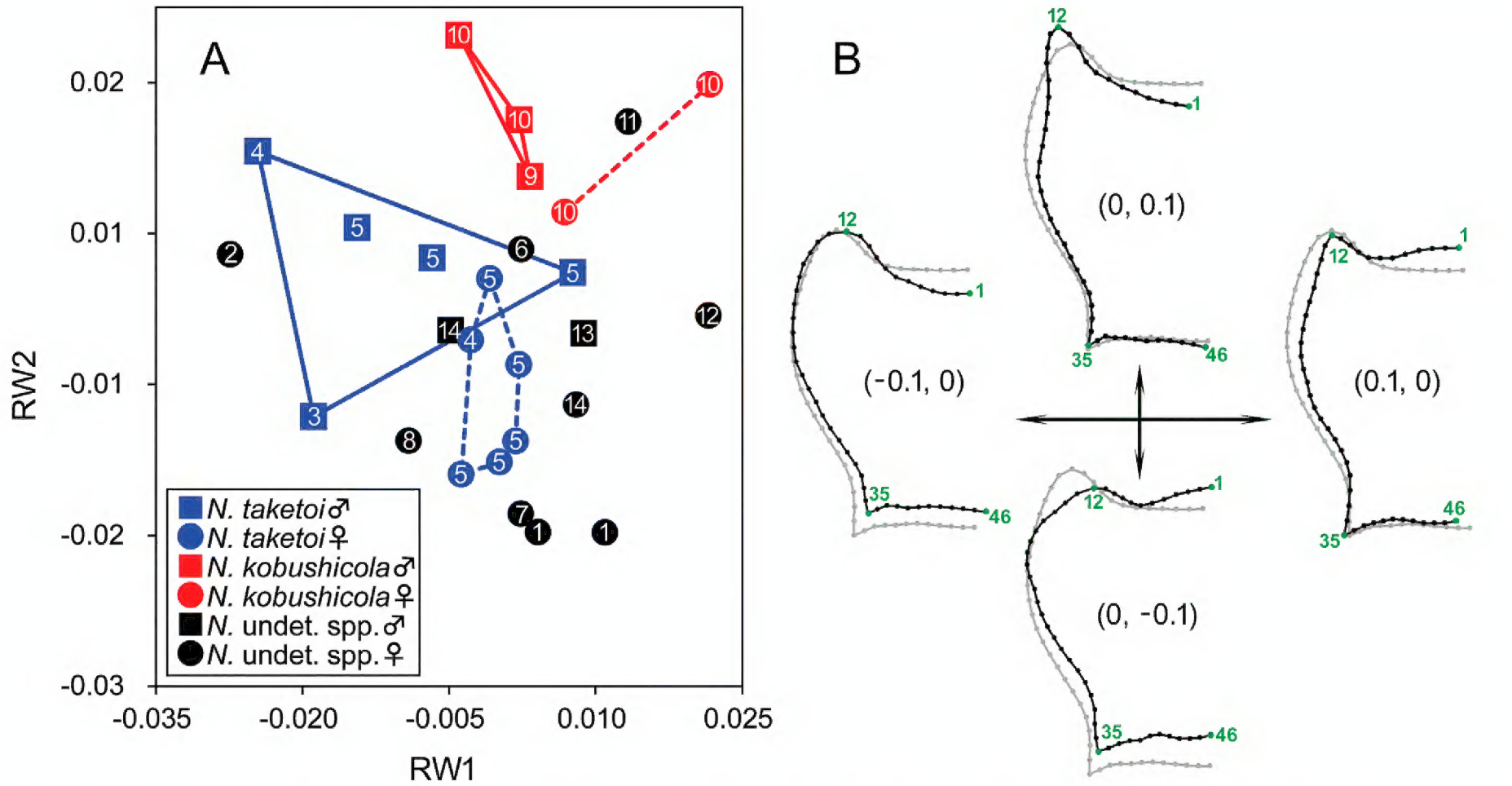

Figure 6. Scatterplot of RW1 and RW2 for the pronotum (**A**) and representations of extreme shape along each axis (**B**). In (**A**), numbers within the symbols indicate that the respective specimen was obtained from the collection site with the same number in Fig. 1. In (**B**), each shape with coordinates in parentheses is shown on the mean shape, which is shown in gray.

IV–VI with two to three setae on each lateral side. Male sternite VII with two to three setae on each lateral side.

***Male genitalia*:** Laterobasal lobes semi-spherical; inflated lobes directed ventrally, not covering the aedeagal apex on lateral views. Lateroapical lobe markedly wide on dorsal view, with the base as wide as or slightly wider than the width of the base of the dorsoapical lobe; anterior and posterior corners protruding in apical and basal directions, respectively, resulting in T-shaped dorsoapical lobes on dorsal view. Dorsoapical lobe with a protrusion on the dorsobasal part; the protrusion directed dorsobasally, not bent; apex of the dorsoapical lobe in a Y-shaped bifurcation on dorsal view; each of the bifurcated apices larger than the protrusion on the dorsobasal part. Dorsobasal surface near the ostium only slightly or not at all swollen. Gonopore protrusion directed ventrally.

Discussion

This study demonstrates the utility of the endophallus in species- and subgenus-level taxonomies of the focal species. Based on this genital morphology, a new species could be distinguished from specimens previously treated as *N. taketoi*. This determination was consistent with the external morphology of the specimens and the results of the morphometric analysis. The results also provide insights into the autapomorphy of the subgenus *Falcinebria*, to which *N. taketoi* and *N. kobushicola* belong. This subgenus was established by Ledoux and Roux (2005), with *N. reflexa* as the type species, but its morphological definition was unclear. Most morphological characters listed as common to members of the subgenus are shared by many species of other *Nebria* subgenera. However, the gonopore protrusion is a feature found only in *N. reflexa* and related *Nebria* species in which the endophallus was examined (e.g., Ledoux and Roux 2005; Sasakawa and Kubota 2006; Sasakawa 2020). In this study, the gonopore protrusion was successfully inverted in one specimen of *N. kobushicola*. Although it could not be successfully everted in the *N. taketoi* specimens examined in this work, the similarity around the gonopore protrusion between the endophallus of *N. taketoi* (Fig. 4F) and the unsuccessfully everted endophallus of *N. kobushicola* (Fig. 5B) implies that *N. taketoi* also has the gonopore protrusion. Thus, the gonopore protrusion can probably be considered an autapomorphy of *Falcinebria*. Future studies should examine the endophallus of other members of the subgenus, especially species from Taiwan and mainland China (Ledoux and Roux 2005).

It is noteworthy that *N. kobushicola* shares two putative apomorphic characters of endophallus with *N. niohozana* Bates, 1883 and *N. dichotoma* Sasakawa, 2020, species previously treated as *N. reflexa*, but not with *N. taketoi*. The first is the T-shaped laterobasal lobes reported in *N. niohozana* and *N. dichotoma*; among *Nebria* species in which the endophallus was examined, T-shaped lobes were found only in *N. niohozana* and *N. dichotoma* and were therefore considered a synapomorphy uniting the two species (Sasakawa 2020). The second character is a dorsoapical lobe with a largely bifurcated apex, reported only in *N. dichotoma*. One possible interpretation of this result is that these morphological similarities reflect phylogenetic relationships among species. If so, the ancestor of species previously regarded as *N. taketoi* (i.e., *N. taketoi*, *N. kobushicola*, and specimens treated as *N. taketoi*) was morphologically similar to *N. kobushicola*, having evolved from a clade containing *N. niohozana* and *N. dichotoma*. This assumption is consistent with the reports of Habu

(1962) and Nakane (1974), which note that *N. taketoi* is morphologically most similar to *N. niohozana*, based on the character states of the male genital right paramere, setae on the abdominal sternites, and the external appearance. Another possible interpretation is that the similar endophallus structures evolved independently. If the observed character states have an advantage for reproductive success, then morphological convergence of endophallus could occur as a result of sexual selection. Future molecular phylogenetic studies of this group will provide insights into this issue.

Some of the specimens with undetermined species identities were obtained from high-altitude mountains, which are separated from the Hida Mountains and the Okuchichibu and Yatsugatake mountains, where *N. taketoi* and *N. kobushicola* occur (Fig. 1). The collection sites at the Iide Mountains are > 200 km away from the other localities. Consequently, some of these specimens may be species other than *N. taketoi* and *N. kobushicola*, but this remains to be confirmed in additional studies.

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Supplementary material 1

Supplementary information

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